2007

Phytoplankton blooms in the Ross Sea, Antarctica: Interannual variability in magnitude, temporal patterns, and composition

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Phytoplankton blooms in the Ross Sea, Antarctica: Interannual variability in magnitude, temporal patterns, and composition

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Received 11 July 2006; revised 4 May 2007; accepted 29 May 2007; published 23 August 2007.

[1] The continental shelf of the Ross Sea, Antarctica, is a unique region within the Southern Ocean. Phytoplankton growth is believed to be seasonally limited, first in austral spring by irradiance, and then in summer by biologically available iron. It also is historically known to have taxonomically distinct regimes: the south-central portion is dominated by *Phaeocystis antarctica* and to the west diatoms are abundant. We measured photochemical yield to interpret the health of the phytoplankton assemblage from 2001–2004 and interfaced these measurements with satellite remote sensing of pigments. The bloom of 2001–2002 was similar in both temporal and spatial distributions to the climatological mean of the Ross Sea, with a peak in biomass being observed in mid-December within the Ross Sea polynyas; F_v/F_m values averaged 0.43. We found high (0.50–0.65) F_v/F_m for most of the seasonal phytoplankton bloom for 2002–2003, suggesting that it was not seasonally iron limited. An unusual, large bloom occurred during 2003–2004, with an initial bloom of *P. antarctica* during austral spring followed by an extensive diatom bloom in summer that may have been enhanced by an intrusion of modified circumpolar deep water. On the basis of an analysis of the historical SeaWiFS records, accumulation of phytoplankton biomass in February may occur approximately every 2–4 years, potentially being a significant source of carbon on the continental shelf.

Citation: Peloquin, J. A., and W. O. Smith Jr. (2007), Phytoplankton blooms in the Ross Sea, Antarctica: Interannual variability in magnitude, temporal patterns, and composition, *J. Geophys. Res.*, *112*, C08013, doi:10.1029/2006JC003816.

1. Introduction

[2] The Southern Ocean carbon cycle is critical to global climate because it represents an area of intermediate and deep-water formation, sequesters carbon, and is believed to be particularly sensitive to climatic fluctuations [*Sarmiento and Orr*, 1991; *Sarmiento et al.*, 1998, 2004]. The primary delimiting current, the Antarctic Circumpolar Current (ACC), is forced clockwise around the Antarctic continent by prevailing westerly winds. The Southern Ocean is the largest high-nutrient, low-chlorophyll (HNLC), region although biomass is higher in coastal, shelf, frontal and ice-edge regions [*Sullivan et al.*, 1993; *Moore and Abbott*, 2000]. In spring, phytoplankton growth is limited by irradiance [*Smith et al.*, 2000], but in summer it may be limited by iron, even on the continental shelf [*Sedwick and DiTullio*, 1997; *Sedwick et al.*, 2000; *Olson et al.*, 2000]. Deposition of iron from aeolian dust is limited in this area (*Fung et al.*, 2000), and biomass in spring is approximately four times that is normally found in summer [*Smith et al.*, 2003].

[3] The Ross Sea, Antarctica is a particularly productive region of the Southern Ocean system and supports a predictable phytoplankton bloom [*Comiso et al.*, 1993]. The phytoplankton bloom is initiated in late October [*Smith and Gordon*, 1997; *Arrigo et al.*, 1998], and reaches maximal concentrations in December [*Smith et al.*, 2000]. Primary productivity follows a similar trend, with the maximum occurring in December [*Smith et al.*, 2000]. The Ross Sea has been historically characterized by taxonomic heterogeneity, with phytoplankton assemblages having distinctly different composition in two separate regions. *Phaeocystis antarctica*, a haptophyte with a multiphasic life cycle, typically dominates the phytoplankton assemblage in the south-central portion of the Ross Sea polynya whereas diatoms often dominate along the coast of Victoria Land and near ice edges [*DiTullio and Smith*, 1996; *Arrigo et al.*, 1999; *Smith and Asper*, 2001]. These floristic trends have not been attributed to a single nutrient or physical feature [*Arrigo et al.*, 1999; *Olson et al.*, 2000; *van Hilst and Smith*, 2002; *Hales and Takahashi*, 2004]. *Arrigo et al.* [1999] and *Smith and Asper* [2001] found deeper mixed layers in areas dominated by *P. antarctica* and shallower ones in those dominated by diatoms. They believed that the taxonomic variability was primarily driven by the efficiency of light harvesting under different light regimes. However, *van Hilst and Smith* [2002] found no differences in the photosynthetic responses in areas dominated by the two taxa, suggesting that light harvesting was not the only force driving the taxonomic variability. They instead, suggested that complex interactions including vertical mixing processes and trace metal limitation drive

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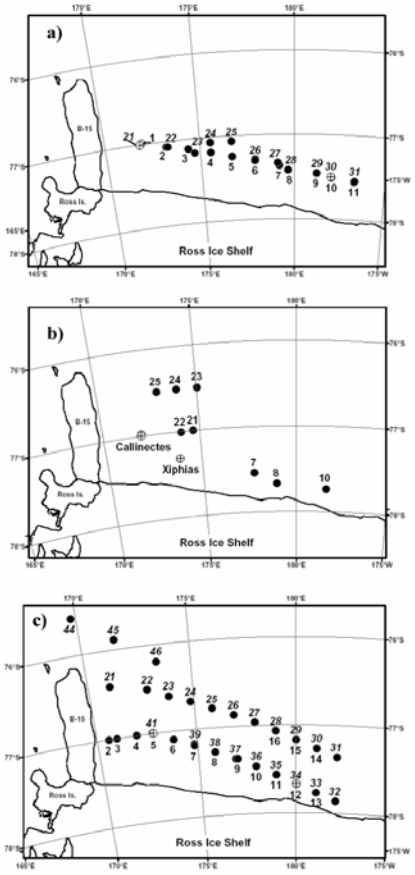

Figure 1. Sampling stations for the IVARS program in (a) 2001–2002, (b) 2002–2003, and (c) 2003–2004.

these floristic trends. It is clear, however, that the taxonomic distribution has profound biogeochemical consequences on vertical flux and elemental ratios of biogenic material [*DeMaster et al.*, 1992; *Smith and Dunbar*, 1998; *Arrigo et al.*, 1999].

[4] The processes governing export are complex, as temporal offsets in primary production, biomass accumulation and export occur [*Smith and Dunbar*, 1998; *Asper and Smith*, 1999; *Collier et al.*, 2000]. This is especially true for regions dominated by *P. antarctica*, as large, intact colonies passively sink (rather than sinking as fecal pellets generated during grazing) toward the end of the seasonal bloom [*Bautista et al.*, 1992; *Asper and Smith*, 1999]. It is also believed that a large portion of *P. antarctica*-derived export is largely remineralized by heterotrophic bacteria within the water column [*Asper and Smith*, 1999], although it has also been suggested that austral spring flux events transport significant amounts of viable cells to depth [*DiTullio et al.*, 2000]. Carbon export in the Ross Sea from diatom-dominated areas, however, appears to be dominated by rapidly sinking fecal pellets produced during zooplankton grazing [*Dunbar et al.*, 1998]. Diatom production is often linked with rates of higher export in Southern Ocean regions [*Boyd and Newton*, 1995], but not always [*Landry et al.*, 2000]. Efficiency of carbon export within areas of high diatom production may be further complicated by a dependency on the specific taxonomic composition of the phytoplankton assemblage [*Smith and Asper*, 2001; *Green and Sambrotto*, 2006].

[5] The objectives of this study were to monitor the maximum photochemical yield of the natural phytoplankton assemblage in December and February over three years in the Ross Sea, using variable fluorescence measurements. The interannual variability in biomass and taxonomic composition was also investigated in the southern Ross Sea. The large-scale trends in phytoplankton biomass were also assessed with remote sensing image analysis of chlorophyll *a*.

2. Materials and Methods

2.1. Study Site

[6] Data for this study were collected in conjunction with an investigation of the Interannual Variability in the Ross Sea (IVARS) program focusing on net community production [*Smith et al.*, 2006]. A total of 80 stations were sampled over three years (generally two cruises per year, in December and February). During 2002–2003 heavy ice caused logistical problems, and only two stations were sampled in February. The spatial coverage of IVARS cruises typically extended from 170°E–176°W and from 76°S–77.5°S (Figures 1a, 1b, and 1c). Six cruises were conducted in the Ross Sea, Antarctica in December and February from 2000–2004 using the USCGC *Polar Star*, USCGC *Polar Sea*, and RVIB *N.B. Palmer* (Table 1). Water was collected using 10-L Niskin bottles mounted on a rosette frame that also held a SeaBird 911+ CTD, a Chelsea fluorometer, and a biospherical photosynthetically active radiation sensor. Profiles of temperature, salinity, irradiance, and fluorescence were collected at each station. Most casts from 2002–2003 were either corrupted or unavailable owing to a loss of the rosette. Only hydrographic data from 2001–2002 and 2003–2004 will be used.

[7] During the time period of 2000–2004, a series of large icebergs calved off the Ross Sea Ice Shelf and were present in the Ross Sea. In March 2000 a large (295 km × 40 km) iceberg named B-15 calved from the ice shelf and remained grounded between Ross and Franklin Islands from 2000 to 2004 [*Arrigo and van Dijken*, 2003] (Figures 1a, 1b, and 1c). In September 2002 another iceberg designated C-19 (32 km × 200 km) calved off of the same ice shelf [*Arrigo and van Dijken*, 2003]. After calving, it proceeded northward and grounded near Pennell Bank and remained there until February of 2003. It continued to move northward and exited the Ross Sea by the following summer [*Arrigo and van Dijken*, 2003]. The presence of these large icebergs is believed to cause changes in local circulation and heat budgets, which in turn impacted ice concentrations in the Ross Sea (M. S. Dinniman et al., The influence of sea ice cover and icebergs on circulation and water mass formation in a numerical circulation model of the Ross Sea, Antarctica, submitted to *Journal of Geophysical Research*, 2007) (hereinafter referred to as Dinniman et al., submitted manuscript, 2007).

2.2. Station Measurements

[8] At each station water samples (~0.25–0.50 l) were taken from up to 12 depths in the water column for chlorophyll *a* analysis. Samples were collected on glass fiber filters (~0.7 μm) and polycarbonate filters (20 and 5 μm) to

Table 1. F_v/F_m Values at the Surface and at 30 m[a]

Year	Month	Dates	F_v/F_m (0 m)	n	F_v/F_m (30 m)	n
2001	December	19–21 December	0.416 (0.04)	11	...	...
2002	December	23–28 December	0.428 (0.05)	7	0.469 (0.05)	6
2003	February	21 February	0.533 (0.06)	2	0.559 (0.08)	2
2003	December	26–30 December	0.367 (0.17)[b]	14	0.493 (0.07)	12
2004	February	3–9 February	0.277 (0.05)[b]	19	0.441 (0.06)	13

[a]The number of samples that entered the calculation of the mean is designed by n and standard deviations of the mean are in parentheses.

[b]Surface samples during 2003–2004 were determined to be statistically significantly different ($\alpha < 0.05$) from other samples taken from surface waters during similar months. No differences were detected between other years or in deeper (30 m) water.

determine the particle size distribution. Filters were placed directly into 90% acetone and sonicated for 15 min on ice. Fluorescence was analyzed on a calibrated Turner Designs Model 10AU fluorometer before and after acidification (to correct for phaeopigment interference [*Holm-Hansen et al.*, 1965]).

2.3. PAM Fluorometry

[9] Evaluation of the quantum yield of photochemistry by the use of fluorometry has been shown to be a powerful tool to assess the physiological status of surface phytoplankton [e.g., *Behrenfeld et al.*, 1996]. Nearly all fluorescence measured at physiological temperatures stems from PSII light harvesting complexes (chlorophyll). Measuring fluorescence and relating it to photochemistry is based on the assumption that a photon absorbed by chlorophyll will have one of three fates: to be used in photosynthesis, dissipated as heat, or reemitted at a longer wavelength as fluorescence. These cellular processes are competitive; by measuring fluorescence, the relative importance of photochemistry can be estimated and insight gained into the physiological heath of the phytoplankton assemblage [*Butler*, 1978; *Kolber and Falkowski*, 1993].

[10] The fluorescence yield from PSII is highly variable and dependent on the physiological state of the phytoplankton cell, which can be affected by a number of factors, including light and nutrient stress. The maximum potential quantum yield from PSII (when all reaction centers are open) is referred to as

$$F_v \Big/ F_m = \left[(F_m - F_o) \Big/ F_m \right]. \quad (1)$$

F_m is the point at which the fluorescence is maximal (all reaction centers are closed), and F_o is the initial determination of fluorescence. F_v is the variable fluorescence term and is the difference between F_m and F_o. The physiological maximum for F_v/F_m for fully functional phytoplankton has been empirically determined to be approximately 0.65 [*Kolber et al.*, 1988] and decreases with the onset of stressful environmental conditions. At low irradiance PAM measurements of F_v/F_m are approximately 20% higher than those determined from FRF, but appear to converge with increasing light intensity [*Suggett et al.*, 2003]. This difference is likely caused by the saturating light pulse and spillover into the first electron carrier, Q_A, allowing multiple turnovers of the photosystem.

[11] PAM measurements were made with a prototype of a submersible unit (SubPAM; Walz) that we used as a benchtop instrument. The SubPAM differs from previous PAM instruments because a photomultiplier tube (PMT) was integrated to enhance the received signal, allowing us to make measurements in both low and high phytoplankton biomass regimes. Samples for the optimal yield of photochemistry (F_v/F_m) were taken from 5 to 30 m. Water was sampled from Niskin bottles, placed on ice, and kept under low light ($\sim$5–10 μmol photons m^{-2} s^{-1}) until measurement (approximately 30 min). The PAM sampling chamber was kept on ice to minimize sample temperature stress. Samples (60 mL) were loaded into the chamber by gravity or by weak pressure from a syringe and measured three times. To obtain F_v/F_m values, the saturation pulse ranged from 0.8 to 1.0 s, and care was taken to insure that the saturation pulse fully achieved the maximum fluorescence. Student's t-tests were used to determine statistical significance between results (α value set a priori at $p < 0.05$).

2.4. Remote Sensing Image Analysis

[12] Sea-viewing Wide Field of View Sensor (SeaWiFS) weekly (8-day) mean chlorophyll concentration data were provided by the NASA/Goddard Earth Sciences (GES)/Distributed Active Archive Center (DAAC) from November to February. Level-3 global Standard Mapped Images at 9 km resolution were used with the OC4 (version 4) calibration, which is the one most recently used by the SeaWiFS project [*Patt et al.*, 2003]. The WimSoft program was used to manipulate and extract numerical data from the images. Data were extracted and binned from 77°S to 77.5°S and from 172°E, 175°E, 178°E and 179°W for all three years of the study. SeaWiFS estimates of chlorophyll a were extracted from four longitudinal lines for the three years of our study. We averaged the values from 77.0°S to 77.5°S. Monthly images were also analyzed from 1997–2004 for the months of November, December, January, and February. Data were extracted from 76.5°S to create the full time series.

3. Results

3.1. Surface F_v/F_m

[13] Surface samples (5–30 m) for five cruises were compared (Figure 2 and Table 1); there were no PAM measurements from February 2002. In December there was little longitudinal structure. In December 2001 F_v/F_m increased with eastward direction and reached a maximum (0.51) at 177°E and declined toward the eastern Ross Sea. Mean values were 0.42, and F_v/F_m reached the lowest value (0.34) at 176°W. In December, 2002 the area of open water was greatly reduced [*Smith et al.*, 2006] owing to changes in local surface circulation patterns and the reduction in wind-

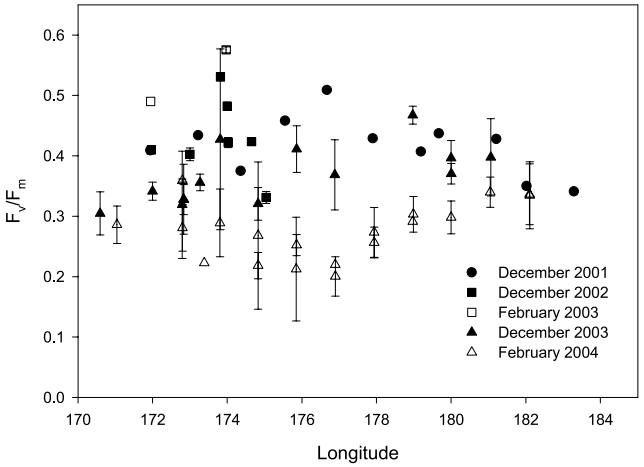

Figure 2. Surface F_v/F_m values (5–10 m) for the phytoplankton bloom of 2001–2002, 2002–2003, and 2003–2004. Error bars represent the standard error around the mean for three replicate measurements of a sample.

driven losses of ice driven by large grounded icebergs [*Arrigo and van Dijken*, 2003]. Thus our sampling regime was limited to open water found in the western portion of the Ross Sea [*Smith et al.*, 2006]. Samples exhibited relatively high F_v/F_m values, averaging 0.43 (±0.05), similar to the December 2001 mean value (0.42) despite the difference in spatial coverage of ice concentrations between the two years. The 30 m F_v/F_m (0.47 ± 0.05) for December 2002 is similar to the surface value, suggesting that there was not substantial long-term photoinhibition when we made our measurements. In February 2003 F_v/F_m was higher in surface waters (0.53 ± 0.06) compared with measurements taken earlier in the season. The following season (2003–2004), surface F_v/F_m in December was low compared to previous years (0.37 ± 0.17), the lowest mean surface value that we measured was found in February (0.28 ± 0.05; Table 1). The transect of February 2004 also showed the most variability in longitudinal structure. The lowest measured value was 0.20 (±0.03) at 176.9°E. December and February sampling periods of 2004 were significantly lower than those measured in previous years ($p < 0.05$). No difference was detected in our observations of F_v/F_m in deeper waters (30 m) for any year or sampling interval.

3.2. Phytoplankton Assemblage

[14] During 2001–2002 December surface Chl *a* concentrations ranged from 2.7 to 12.1 μg L^{-1}, and the average value was 5.76 μg L^{-1} (Table 2). Two months later February surface Chl *a* concentrations were approximately the same, with the surface Chl *a* averaging 5.62 μg L^{-1} and a range from 2.30 to 7.64 μg L^{-1}. In 2001–2002 the largest size fraction (>20 μm) on average accounted for 47 and 61% of total surface Chl *a* in December and February, respectively. The smallest size fraction (<5 μm), in contrast, contributed 38 and 32% of surface Chl *a*. This suggests that the phytoplankton size structure remained relatively unchanged from December to February. Taxonomic data for December of 2001 show that single-celled phase of *P. antarctica* was the numerically dominant form and taxon of phytoplankton in late December [*Peloquin*, 2005]. Colonial *P. antarctica* was dominant at two stations at the western and eastern part of the Ross Sea, but its distribution did not appear to follow any distinct pattern. When both forms of *P. antarctica* are considered together, they accounted for >80% of the assemblage composition by abundance [*Peloquin*, 2005]. Diatom numbers increased from west to east and peaked at 178°W where they contributed ~20% of the total cell numbers. Accessory pigment and biogenic silica concentration data show that diatoms increased in importance and dominated the assemblage in February [*Smith et al.*, 2006].

[15] The seasonal bloom of 2002–2003 was much smaller when compared to the previous year. Average surface chlorophyll *a* concentrations were 2.13 μg L^{-1}, with a maximum and minimum of 6.38 and 0.34 μg L^{-1}, respectively (Table 2). In February surface chlorophyll *a* was again approximately equal to that of December, with a mean concentration of 2.46 μg L^{-1}. We were only able to sample two stations in the Ross Sea in February, so the maximum and minimum represent these two stations (3.12 and 1.80 μg L^{-1}). The contribution of the >20 μm size fraction in December and February was 32 and 30%, respectively. Small phytoplankton (<5 μm) were the largest component of Chl *a* during 2002–2003 (50 and 77%; Table 2). It appears that this relatively weak bloom was sustained until late February and that the contribution of the largest size fraction was relatively constant throughout. However, the smallest size fraction became relatively more important by February owing to a shift from the <20 and >5 μm size fraction into the <5 μm size fraction. We only have taxonomic data for 3 stations in December 2002 (data not shown). Diatoms dominated the phytoplankton assemblage for these three stations, representing 80–100% of the phytoplankton cells counted.

[16] Accumulation of phytoplankton biomass was highest in 2003–2004 and was well established by December. In Decem-

Table 2. Average Size Distribution of the Surface Phytoplankton Assemblage Determined by in Situ Chl *a* Concentration and the Relative SeaWiFS Estimate of Chl *a* for 3 Years of the IVARS Program[a]

Year	Month	Total Chl *a*, μg L^{-1}	>20 μm, μg L^{-1}	<5 μm, μg L^{-1}	Percent > 20 μm	Percent < 5 μm	n
Year 1 (2001–2002)	December	5.76 (2.6)	2.39 (0.8)	2.62 (2.8)	47.12 (22.1)	38.77 (30.5)	11
	February	5.62 (5.6)	3.63 (1.7)	1.59 (1.4)	61.48 (16.4)	32.68 (30.3)	17
Year 2 (2002–2003)	December	2.13 (2.0)	0.94 (1.2)	0.87 (0.7)	31.56 (18.1)	49.85 (22.3)	10
	February	2.46 (0.9)	0.79 (0.5)	2.03 (1.4)	30.05 (9.7)	76.96 (29.1)	2
Year 3 (2003–2004)	December	5.22 (2.7)	3.36 (1.7)	1.56 (1.0)	67.20 (17.7)	29.48 (17.1)	13
	February	10.36 (3.5)	6.22 (2.0)	3.28 (1.9)	62.08 (13.4)	30.38 (13.8)	20

[a]Standard deviations of the mean are in parentheses.

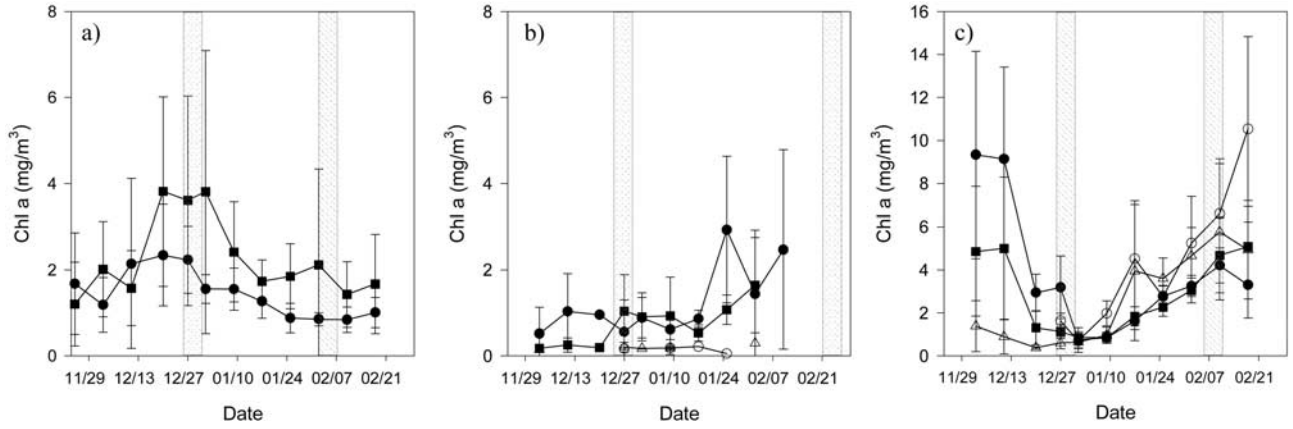

Figure 3. Results from the SeaWiFS estimates of chlorophyll *a* (mg/m^3) for 172°E (solid circles), 175°E (squares), 178°E (triangles), and 178°W (open circles) for (a) 2001–2002, (b) 2002–2003, and (c) 2003–2004. Bars represent the periods of IVARS occupation, and error bars are 1 standard deviation from the mean.

ber 2003, surface Chl *a* ranged from 0.95 to 9.39 μg L^{-1}, with an average of 5.22 μg L^{-1}. Average Chl *a* concentrations in February increased to 10.3 μg L^{-1}, ranging from 4.06 to 15.1 μg L^{-1} (Table 2). The contribution of Chl *a* of the >20 μm size fraction comprised 67.2 and 62.0% of the total Chl *a* in December and February, respectively. Although the bloom increased in concentration from December to February, there was no apparent shift in the assemblage size spectrum. In December 2003, the contribution of colonial *P. antarctica* to the phytoplankton assemblage decreased to the east [*Peloquin*, 2005]. Interestingly, the contribution of the single-celled form of *P. antarctica* paralleled the diatomaceous contribution, with maxima contribution in the easternmost portion of our sampling grid. When the two forms of *P. antarctica* are considered together, they comprise 90–70% of the assemblage. Direct counts of phytoplankton biomass and HPLC-based estimates of diatom showed that diatoms dominated the assemblage in February of 2004 [*Peloquin*, 2005; *Smith et al.*, 2006]. *P. antarctica* was still present in February 2004, but never numerically dominated the phytoplankton assemblage.

3.3. SeaWiFS-Based Bloom Dynamics

[17] In general, SeaWiFS estimates of phytoplankton biomass indicated an initial peak in the western edge of our sampling transect that proceeded east (Figures 3a, 3b, and 3c). In 2001–2002 we sampled the onset of bloom decline at 172°E, but the peak of the seasonal increase at 175°E (and prior to the initiation of the decline; Figure 3a). The decreased magnitude of the 2002–2003 bloom reported by *Smith et al.* [2006] is also reflected in the SeaWiFS chlorophyll distribution. We sampled between two small biomass maxima during 2002–2003, but most of the chlorophyll *a* appears to have accumulated in early January to February. In 2003–2004 there was not a strict seasonal progression toward the east, but it appeared that the western and eastern Ross Sea operated on different timescales (Figure 3c). That is, a large bloom occupied the western portion of our transect in early December; we sampled this when the surface signal in F_v/F_m was declining (Figure 3c). In early January another bloom was initiated throughout the entire transect. We sampled during the period of increasing biomass, which was also reflected in the fluorescence recorded by a series of in situ fluorometers at the mooring sites [*Smith et al.*, 2006]. The areal extent of this accumulation of biomass in February was large and covered most of the open polynya in the southern Ross Sea. This accumulation was also gradual in nature (Figure 3c) suggesting that it is the result of local production and not of lateral advection or progression of another water mass (i.e., a large bloom from the eastern Ross Sea).

3.4. Hydrographic Data

[18] We tested, using temperature and salinity data, whether water mass intrusions corresponded with the presence/absence of accumulation of phytoplankton biomass in February in the Ross Sea transect. In December 2001, we found no evidence for anomalous water mass intrusions (Figure 4a), but in February 2002 there was evidence of slight warmer (~−1.4 to −1.0°C) and more saline water (34.4 to 34.6) within the water column (Figure 4b). In December 2003, one station (Station 1) had elevated temperature (~−0.5°C) at 150 m (Figure 4c). When we returned in February 2004, this high-temperature and high-salinity signal in deeper water was more prevalent (Figure 4d), especially when compared to February of 2002. This signal also appeared to peak at approximately 174°E (Figure 5). We also detected subsurface anomalies from 50 to 200 m (Figure 6) that appear to have similar structure as those in deeper water, but were more restricted; the signal spanned tens of meters rather than being 50–100 m in vertical extent.

3.5. SeaWiFS Historical Record

[19] According to the SeaWiFS record from 1997 to 2004, phytoplankton blooms have occurred in February in the Ross Sea on more than one occasion. The historical record repeatedly shows the build up in phytoplankton biomass during the early bloom months of November and December (Figure 7b) with decreasing concentrations in January (Figure 7b). Three years (1997–1998, 1999–2000 and 2003–2004) contrast the traditionally understood dynamics of phytoplankton biomass accumulation and decline in the Ross Sea (Figure 7a). These three years either exhibit secondary accumulation of biomass (2003–2004;

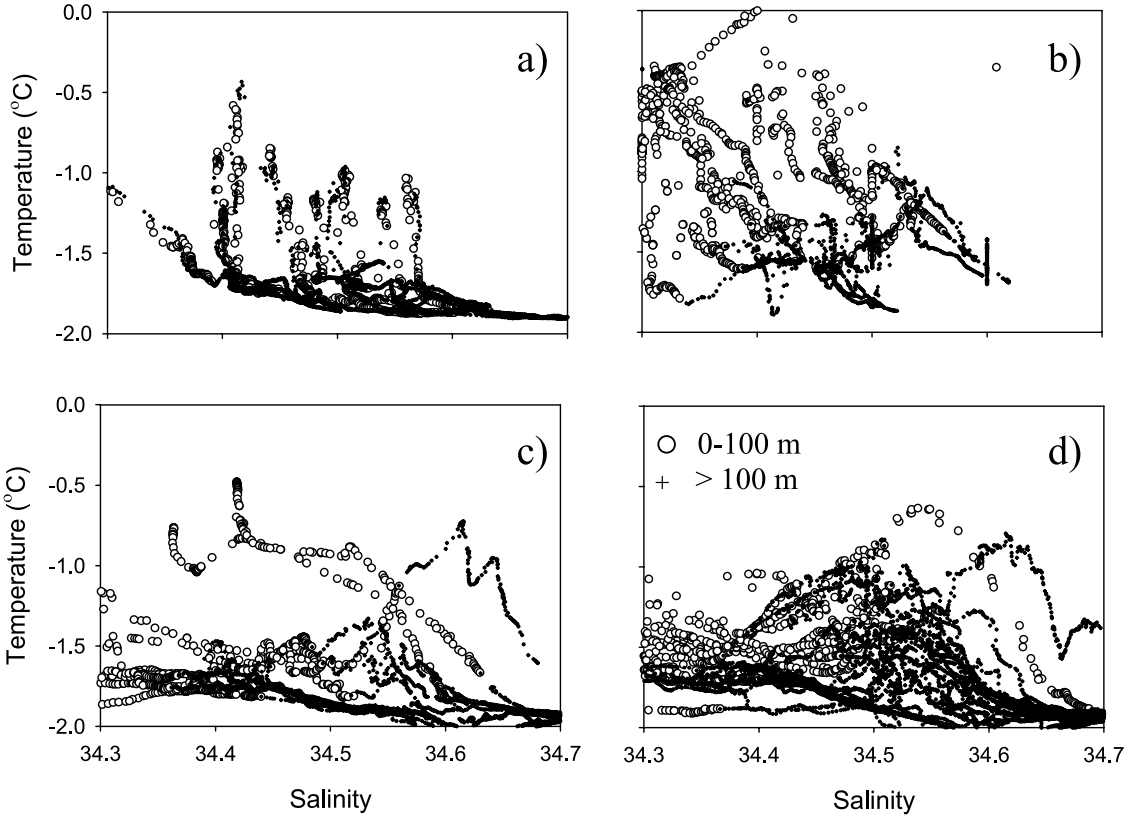

Figure 4. Potential temperature versus salinity plots for (a) December 2001, (b) December 2003, (c) February 2002, and (d) February 2004. Data were extracted from 0- to 500-m CTD casts, and 0- to 100-m data (circles) are plotted separately from those >100 m (crosses). MCDW is characterized by <-1.5°C temperature and salinity between 34.4 and 34.6.

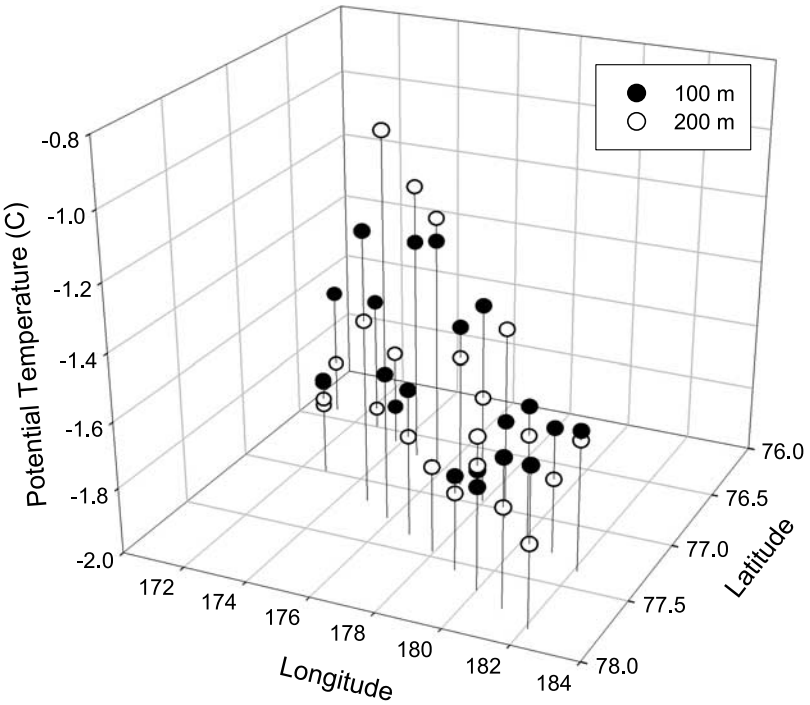

Figure 5. Temperature values (°C) at 100 and 200 m in February 2003.

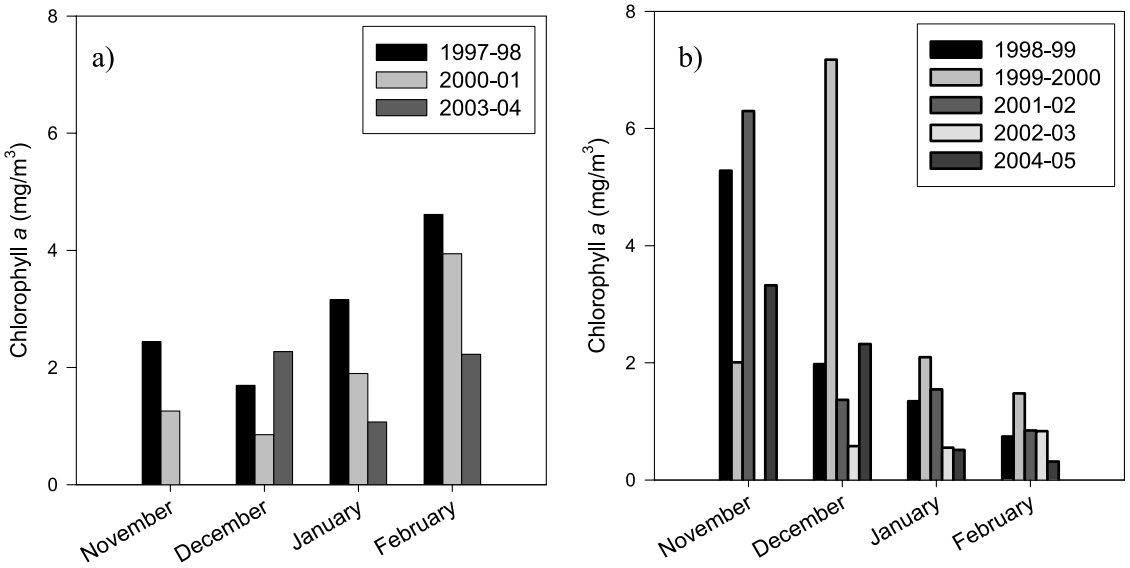

Figure 6. Chlorophyll estimates (mg/m^3) from SeaWiFS averaged from 76.5°S and 172°E–180°E on a monthly basis. Years have been separated according to the timing in the accumulation of phytoplankton biomass: (a) accumulation of phytoplankton biomass occurs in spring-summer and again in February (secondary bloom) or when a maximum occurs in February, and (b) accumulation of biomass occurs in November–December and declines over the course of the summer (traditionally held idea of Ross Sea bloom dynamics).

although the signal is tempered when the 76.5°S transect is averaged from 172°E–180°E) or the primary accumulation of biomass appears to occur in February.

4. Discussion

[20] The Ross Sea, Antarctica is a unique region within the Southern Ocean system. Surrounded by high-nutrient, low-chlorophyll waters of the Antarctic circumpolar current, it is highly productive, particularly in the south, with an average maximum chlorophyll *a* concentration during austral summer of ~6 μg L^{-1} [*Smith et al.*, 2003]. The Ross Sea also is historically known to have taxonomically distinct regimes; the south-central portion is dominated by the Ross Sea polynya and by *P. antarctica* (a haptophyte with colonial and single-celled morphologies), and the west is a region where diatoms are relatively more abundant. There is no generally accepted consensus of the environmental conditions controlling this taxonomic heterogeneity [*Arrigo et al.*, 1999; *van Hilst and Smith*, 2002; *Hales and*

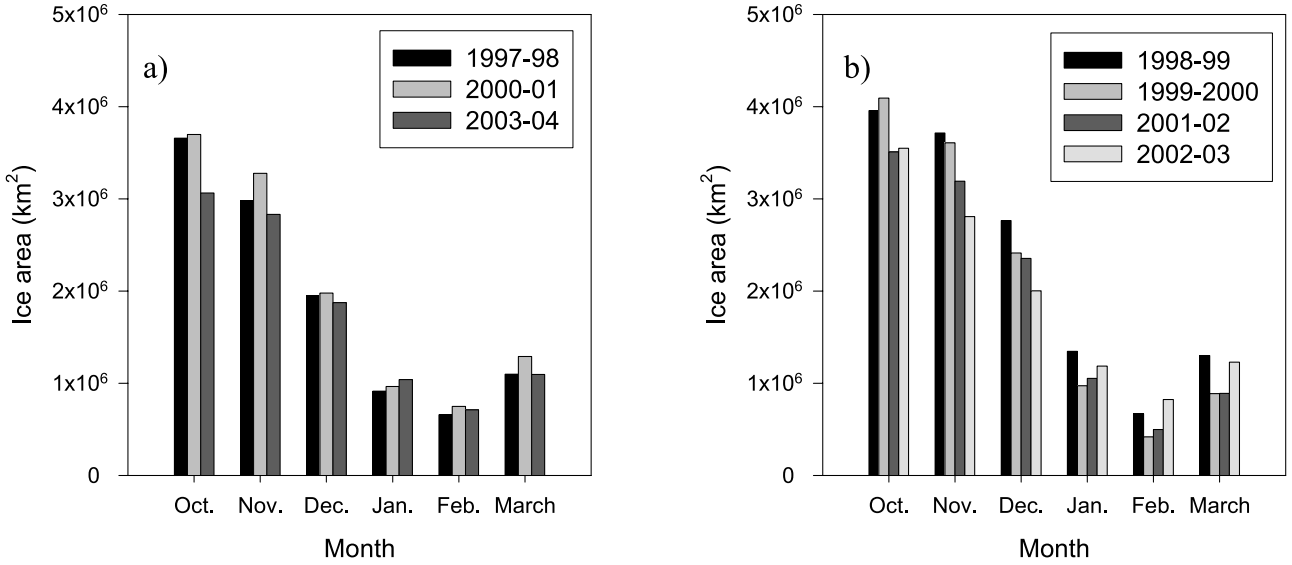

Figure 7. Estimates of ice area (km^2) for years when (a) accumulation of biomass occurs in spring-summer and again in February (secondary bloom) or when a maximum in the SeaWiFS phytoplankton biomass estimate occurs in February, and (b) accumulation of biomass occurs in November–December and declines over the course of the summer (traditionally held concept) as defined in Figures 7a and 7b. (Data are from National Snow and Ice Data Center [*Comiso*, 2007].)

Takahashi, 2004], but light, mixing regimes and micronutrient availability all likely contribute to some degree.

4.1. Interannual Variations in Phytoplankton Blooms

[21] The phytoplankton blooms of 2001–2002, 2002–2003, and 2003–2004 were distinctly different from one another [*Smith et al.*, 2006]. In 2001–2002 a large fraction of the *P. antarctica* occurred as single cells. Mean surface F_v/F_m was still relatively elevated (0.42) with little longitudinal variation, suggesting that areas with higher contribution of diatoms had a physiological state similar to those where *P. antarctica* dominated. It has been suggested that *P. antarctica* has a higher iron quotient when compared to diatoms [*Coale et al.*, 2003; *Sedwick et al.*, 2007], so in general we expected areas dominated by *P. antarctica* to show more severe iron limitation late in the bloom. From the analysis of SeaWiFS images, it appears that when we sampled in December biomass was maximal in the east-central Ross Sea. On the basis of HPLC pigment distributions, it also appeared that diatom contribution to the phytoplankton assemblage was high in the Ross Sea in February 2002 [*Smith et al.*, 2006].

[22] The accumulation of phytoplankton biomass in 2002–2003 was low when compared to the other years and the Ross Sea climatology [*Smith et al.*, 2003]. This was likely due to the presence of large icebergs in the Ross Sea, which are believed to cause changes in local circulation patterns and ice movement [*Arrigo and van Dijken*, 2003; Dinniman et al., submitted manuscript, 2007]. The phytoplankton bloom was dominated by diatoms and did not have F_v/F_m values in February indicative of iron stress. Although this bloom was a fraction of the magnitude observed in other years, SeaWiFS data suggest that there was a minor initial bloom followed by a second, more substantial accumulation of biomass in February, although the errors around this estimate are large (Figure 3b). Indeed, we found surface F_v/F_m values to be slightly higher in February (0.53 ± 0.06) than in December (0.43 ± 0.05), suggestive of an additional input of iron, perhaps in early mid January.

[23] Phytoplankton biomass in 2003–2004 was greater than that in other years of this study. The dominant *P. antarctica* morphology in December was colonial, and the contribution of diatoms increased to the east. The mean surface F_v/F_m was significantly lower than measured in previous years (0.37 ± 0.17), coupled with a large accumulation of chlorophyll *a* [*Smith et al.*, 2006]. It appeared that when we occupied the Ross Sea that biomass had become maximal in early December and we sampled the initial bloom decline (Figure 3c). Furthermore, the magnitude and timing of this initial bloom suggests that the previous year's conditions (2002–2003) affected the early onset and magnitude of the bloom of 2003–2004, perhaps because of high ice concentrations. In February mean surface F_v/F_m was further depressed to 0.28 (±0.05). In 2002–2003, a large accumulation of phytoplankton biomass was detected in February and was dominated by diatoms [*Smith et al.*, 2006]. Unique to this year, however, was the areal extent of the phytoplankton accumulation, as it was nearly as large as the primary bloom and exhibited F_v/F_m values indicative of severe iron stress (Figure 2).

[24] For two of the three years of our study, SeaWiFS detected increased phytoplankton biomass through the beginning of February, although this feature is more impressive in 2003. This 2003 accumulation was also observed by moored sensors and is not an artifact of satellite remote sensing [*Smith et al.*, 2006]. From observations of phytoplankton taxonomy [*Peloquin*, 2005], biogenic silica concentrations, and accessory pigment data [*Smith et al.*, 2006], we know that this bloom comprised large diatoms. Although the absolute magnitude of the February 2003 bloom is appreciable (Figure 3c), the process mediating its formation is far from certain. To our knowledge, accumulation of diatomaceous material in the central Ross Sea have not been documented to this magnitude, nor are they reflected in the Ross Sea climatology [*Smith et al.*, 2003]. Presumably, *P. antarctica* blooms early in the spring because higher ambient iron concentrations provided by winter mixing meet its higher iron requirements (when compared to diatoms [*Coale et al.*, 2003]), along with its ability to photosynthesize and thrive in relatively deep mixed layers [*Arrigo et al.*, 1999]. During December 2003 we found F_v/F_m ratios indicative of iron limitation over the entire transect, and not in just areas dominated by *P. antarctica*.

4.2. Mechanisms for Accumulation of Phytoplankton Biomass in February

[25] The interannual variability within the Ross Sea is appreciable; we sampled three successive years with marked differences in phytoplankton accumulation, spatial extent and composition. Perhaps the most novel finding from this work is the observation during sampling in 2003–2004 of two distinct events (December and February) when phytoplankton biomass substantially accumulated in the mixed layer. Although a similar floristic succession, haptophytes followed by diatoms, has been observed in the ACC [*Green and Sambrotto*, 2006], this trend has never been observed or reported in the Ross Sea, nor is it revealed within the climatology to the extent we observed [*Smith et al.*, 2003]. We also believe the accumulation of biomass in February 2004 was the result of local growth. Data extracted from moorings corroborate the gradual increase in biomass shown in the analysis of SeaWiFS images (Figure 3c) [*Smith et al.*, 2006], so we do not think that we were sampling an advected and or subducted/resurfaced phytoplankton biomass. If phytoplankton were clearly exhibiting iron stress in December, how could a subsequent accumulation of biomass occur in February? Plausible mechanisms for this include: (1) the dominance of a phytoplankton assemblage with low iron requirements, (2) local infusion of iron through mineralization of the initial bloom freeing biologically available iron or increased iron supply from melting ice, or (3) a water mass intrusion (and subsequent introduction of iron into the surface layer from depth).

[26] It is possible that the phytoplankton assemblage that replaced *P. antarctica* had significantly lower iron quotients. Studies have found that *P. antarctica* has higher iron requirements than diatoms [*Coale et al.*, 2003; *Sedwick et al.*, 2007] so the dominance of diatoms late in the austral summer may simply indicate that *P. antarctica* cannot thrive under iron-poor conditions. This type of floristic succession from *P. antarctica* to diatoms has been observed previously in the ACC [*Green and Sambrotto*, 2006]. Iron enrichment

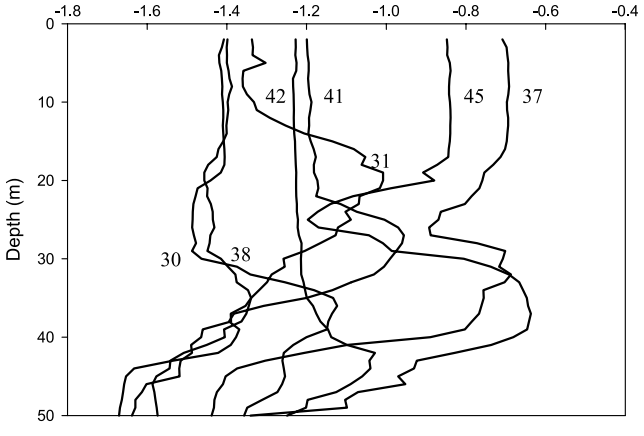

Figure 8. Estimates of monthly changes in ice-covered area (km^2) during a 1-month period in the Ross Sea. Data plotted represent the change of ice from that month to the next. (Data are from National Snow and Ice Data Center [*Comiso*, 2007].)

bottle experiments were conducted in the Ross Sea in summer at two sites to estimate the half saturation constant for *P. antarctica* and diatoms. These studies indicate that diatoms have significantly lower iron half saturation constants (0.008 and 0.004 nM) compared with *P. antarctica* (0.005 and 0.043 nM [*Coale et al. 2003*]). Therefore it is, in theory, possible for diatoms to follow a *P. antarctica* bloom after its termination, provided that there is sufficient iron left in the water column.

[27] The areal extent and magnitude do, however, make this explanation unlikely. The increase in biomass was regional in scale and spanned the main polynya; there would have to have been significant iron remaining in the water column to support this bloom. We do not have water column iron measurements; we do not know what iron concentrations were at the termination of *P. antarctica* bloom. However, since diatoms are among the taxa that respond to iron enrichment experiments in the Southern Ocean [*Boyd et al.*, 2000; *Coale et al.*, 2003], it seems unlikely that they would thrive in the presumed iron-poor waters in the Ross Sea. Diatoms are also believed to be favored under more shallow mixed layers, but we detected no change in mean mixed layer depth (~20 m) between December and February [*Smith et al.*, 2006]. Furthermore, if a taxonomic succession driven simply by iron quotients explain the February increase in phytoplankton biomass, then we expected to see this sort of trend (in scale and magnitude) annually and that's simply not the case. The historically found taxonomic trend is spatial, rather than temporal, with *P. antarctica* dominating in the central Ross Sea and diatoms found near ice edges and the western Ross Sea [*DiTullio and Smith*, 1996; *Arrigo et al.*, 1999; *Smith and Asper*, 2001].

[28] Since the Ross Sea is believed to be seasonally limited by iron [*Sedwick and DiTullio*, 1997; *Sedwick et al.*, 2000; *Olson et al.*, 2000], the fact that a bloom developed in February after the termination of the initial December-based accumulation of biomass suggests that there may be additional inputs of iron to this system in late January. One possible source of iron could be local remineralization of the December *Phaeocystis* bloom. Iron can be recycled in surface waters by bacterial or grazer mineralization, but there are many uncertainties and relatively little is known about rates or controlling mechanisms [*Hutchins et al.*, 1993; *Price et al.*, 1994; *Barbeau et al.*, 1996].

[29] In the Ross Sea, sources of new iron to surface waters come from primarily local origin since rates of atmospheric dust deposition in the Southern Ocean are among the lowest globally [*Prospero*, 1981; *Duce and Tindale*, 1991; *Fung et al.*, 2000]. Vertical transport, deep mixing during winter months and ice melt are mechanisms that bring new iron into surface waters. In 2003, surface waters were less saline than previous years, indicating increased in situ meltwater input. It is possible that ice concentrations and thicknesses (and hence total amount of fresh water) were higher following the spatially restricted polynya of 2002–2003, and there was a higher potential for iron supply from melting ice. Release of iron from ice has been hypothesized to be an important mechanism in the Ross Sea [*Sedwick and DiTullio*, 1997]; however, the polynya was well developed by early January 2004 [*Smith et al.*, 2006]. There was additional loss of ice from the region (either through advection or melting) from December to January (Figure 8), and we cannot completely eliminate the possibility that some biologically available iron was released from meltwater. Rates of ice loss were not abnormally high (Figure 8) on the basis of a regional analysis of ice cover in the Ross Sea, especially when compared with 2000–2001 when seasonal dynamics followed the traditionally held Ross Sea climatology. Additionally, mixed layer salinities (<20 m) were not substantially lower from December to February, 34.17 ± 0.11 and 33.92 ± 0.14, respectively. This suggests that substantial amounts of low-salinity ice melt were not introduced in our study site from December to February.

[30] Vertical transport of iron through upwelling or water mass intrusion may also bring new sources of iron to surface waters. The intrusion of modified circumpolar deep water (MCDW) onto the Ross Sea continental shelf has been well established [*Jacobs et al.*, 1985; *Carmack*, 1990; *Gordon et al.*, 2000; *Hiscock*, 2004; *Hales and Takahashi*, 2004; *Stover*, 2006]. This water mass is a diluted form of Circumpolar Deep Water (CDW), is forced onto the continental shelf and can be found in surface waters [*Hales and Takahashi*, 2004]. MCDW may be a source of iron and is characterized by being warmer (>1° to −1.5°C) and more saline (~34.4–34.6) [*Carmack*, 1977] and may influence the timing and magnitude of the seasonal phytoplankton bloom in the Ross Sea by providing iron to surface waters [*Hiscock*, 2004]. We have evidence of the intrusion of modified circumpolar deep water (MCDW) that is especially strong near the western edge of the February 2003 transect. Despite not knowing the exact micronutrient and macronutrient concentrations of this water in February 2003, in theory, this water mass only has to have elevated biologically available iron concentrations when compared to well-mixed surface waters in order to potentially influence the phytoplankton assemblage. Iron measurements were made in a similar area of the Ross Sea in January 1990, and several of the measurements were made in water mass with MCDW T-S characteristics [*Fitzwater et al.*, 2000]

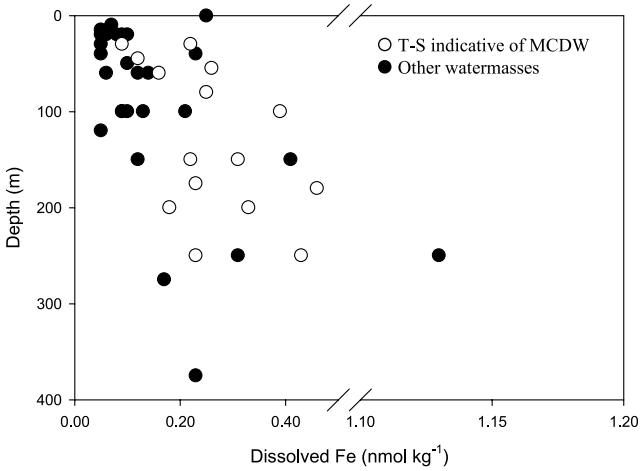

Figure 9. Dissolved iron measurements (nmol kg^{-1}) made in 1990 for water with T-S characteristics indicative of MDCW (open circles) compared with the other water masses in the Ross Sea (solid circles) (data from *Fitzwater et al.* [2000]).

(Figure 9). Two of these measurements were made from shallow water (30 m) with iron measurements of 0.09 and 0.22 nmol kg^{-1}. Iron measurements made >50 m averaged 0.29 nmol kg^{-1} with a range of 0.16–0.46 nmol kg^{-1}. Since iron levels in the summer time in the Ross Sea have been measured between 0.03 and 0.04 nM [*Coale et al.*, 2003] and given the above estimates, 10% replacement of MDCW water would roughly double the dissolved iron concentrations. Although these measurements were not from our year of study, they do prove that MCDW intrusions could represent a substantial increase in surface iron concentrations, dependent on the magnitude and timing of upwelling.

[31] A difficulty with the hypothesis that MCDW could provide enough iron for a large diatom bloom is that stratification remained strong in February, which would restrict the introduction of the Fe-replete waters into the euphotic zone. When we analyzed the temperature signal in February 2003, the waters between 50 and 200 m have pockets of water with a higher temperature, suggesting that some volume of MCDW can reach into the surface layer. *Hales and Takahashi* [2004] also detected entry of this water in surface waters of the Ross Sea in 1996. Interestingly, they detected an intrusion of MCDW and low-salinity surface water separating two distinct areas dominated by *Phaeocystis* to the west and diatoms to the east. They also observed MCDW intrusions occurring with small-scale patchiness that would be missed by traditional oceanographic surveys such as those done as part of the IVARS study.

[32] One marked difference between February of 2001, when the phytoplankton trends track the climatology, and 2003 is the presence of MCDW within our study site. There was very little evidence of MCDW in February 2001 (Figure 4c). Upwelling or water mass intrusions influencing on-shelf primary and secondary productivity has been well established in other Antarctic regions as well [*Prezelin et al.*, 2000; *Bindoff et al.*, 2001; *Sambrotto et al.*, 2003]. Presumably, UCDW is entrained into surface waters through persistent wind-driven mixing and infuses surfaces waters with sufficient biologically available iron impacting local biogeochemistry.

[33] We cannot unequivocally prove that the injection of MCDW into surface waters influences the timing and magnitude of the accumulation of biomass in February 2004. We do know, however, that blooms in February have occurred at least two other times since 1997 according to the SeaWiFS historical record and that these events do not appear to be related with a regional analysis of anomalous or late ice melt years (Figure 8). If these accumulations are due to taxonomic succession and dependent on varied iron quotients, as seen in other areas like the ACC [*Green and Sambrotto*, 2006], then we need to better understand why these processes dominate certain years and not others.

[34] In conclusion, the phytoplankton blooms we observed in three successive years had distinct characteristics in dominant flora, timing and magnitude. The regulation of the spatial distribution of *P. antarctica* and diatoms in the Ross Sea remains unclear, and the magnitude of the February bloom of 2003–2004 was unexpected, and thus adds another layer of complexity to the characteristics of the seasonal cycle. We also detected a temporal separation, as well as spatial heterogeneity, between the two taxa that had not been previously observed in the Ross Sea. Furthermore, MCDW intrusions onto the shelf of the Ross Sea may be substantial enough to support appreciable diatom bloom. The fact that large blooms appear in February at least two other times in the historical record further suggests that this feature is important in the biogeochemical functioning of the Ross Sea. Further investigation of these issues is critical, as the taxonomic distribution has profound biogeochemical consequences and strongly controls the magnitude of vertical flux and elemental removal ratios [*DeMaster et al.*, 1992; *Smith and Dunbar*, 1998; *Arrigo et al.*, 1999]. As such, it affects the larger-scale partitioning of elements in the Ross Sea and how carbon is ultimately utilized by higher trophic levels. Furthermore, particulate carbon production occurring later in the season may have an enhanced probability of being entrained during deep water formation. This may have an impact on the potential for carbon sequestration within the Ross Sea.

[35] **Acknowledgments.** This project was supported by a grant from the National Science Foundation (OPP-0087401). We thank Orbimage for the SeaWiFS mission and the SeaWiFS Project for data analysis and availability. We thank S. Polk and J. Dreyer for technical assistance and to the many volunteers that worked with the IVARS program. This paper was greatly improved by valuable input from P. Ralph, H. Ducklow, T. Moisan, D. Bronk, B. Hales, and one anonymous reviewer. This is VIMS contribution 2848.

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